

A Study of the Reproductive Cycle in the California Acmaeidae (Gastropoda)

Part II

by

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(Plates 15 to 17)

Subgenus NOTOACMAEA IREDALE, 1915

Acmaea persona ESCHSCHOLTZ, 1833

Ecology: — This is a high intertidal limpet which lives as high as or higher than the other high form, *Acmaea digitalis* Eschscholtz, 1833, but is much less eurytopic, never being found below zone 1. It prefers rocky areas which afford it dark crevices and under-surfaces where it can spend the daylight hours since it is a nocturnal form and feeds only at night or on heavily overcast days. It is a scraper of what appear to be bare rock surfaces since little macroscopic algae can live with such minimal exposures to wetting by the sea. Typically its habitat is seldom, if ever, submerged and receives only splash and spray from the surf at high tide. *Acmaea persona* was studied primarily from the rocky point south of Rockaway Beach, San Mateo County, California (37° 30' 25" N; 122° 30' W) where the species occurs in moderate numbers on the highest of the intertidal rocks. Here the animals are found between five and six feet above the zero tide level and extend down to the highest populations of the barnacle, *Balanus glandula* Darwin, 1854. *Acmaea digitalis* is found up to the middle of this range but disappears above that, leaving only the high littorine, *Littorina planaxis* Philippi, 1847, as a frequent co-resident with *A. persona*. This shore is exposed to the full radiation of the sun, and the tops of the rocks are always burned free of any algae, the only plant material present here being the unicellular algae cast up by the surf. Along the bases of the rocks, however, and in shaded crevices there is often a film of algae which may, give the rock a greenish sheen.

Collections: — The initial collections of this animal consisted of only a few specimens (usually five or less) every two weeks. Beginning in late August, 1950, the number of these was increased to ten per sample, and this was continued throughout the remainder of the study. The entire investigation extended from November 19, 1949, through April 16, 1952, during which period a total of 459 animals was examined: 127 males, 128 females, and 204 indeterminate. Despite this small sample size, complete reliance can be placed in the data assembled for this species since it shows a simple annual reproductive cycle in which the population participates very much as a unit.

Results: — This species (Plate 15) has a clear-cut annual reproductive cycle which is characterized, at Rockaway Beach, by a single complete spawning during the latter part of March and the first part of April. This spawning may be preceded by a partial spawning earlier in the year as occurred in 1951 and 1952. Such a partial spawning leaves the gonads reduced in turgor but by no means completely spawned, perhaps only one-third to one-half of the gametes having been released. Subsequent to this early partial spawning, the gonad is more or less redeveloped to a ripe condition in which state the complete spawning occurs. This latter spawning is an unusually complete discharge of gametes, the ovary retaining only a few residual eggs and the testis having only small gray patches of sperm remaining. During the succeeding months, May and June, these residual gametes disappear, probably due to breakdown and resorption, so that by mid-June or earlier the entire population has become sexu-

ally indeterminate. It remains in this condition until late October at which time the gonads begin redevelopment and by the last of November all animals are again of determinate sex. The development of the gonad continues until a fully ripe condition is reached at which time either a complete spawning (1950) or a partial spawning (1951 and 1952) occurs. Beginning in January, 1952, and continuing into April, 1952, collections were obtained through the courtesy of Dr. Rudolf Stohler, from several points in Sonoma and Mendocino Counties, California. Data obtained from these samples indicate that Acmaea persona from these more northern areas exhibits essentially the same reproductive cycle as those from the region of San Francisco.

Analysis of Environmental Conditions Coincident with Spawning: —

Plate 15 shows that the redevelopment of the gonad of this species begins in late October and early November. It is at this time that the new gametes become visible in the exposed gonad at moderate magnification. As has been previously indicated, October is a critical month for both air and water temperatures for it is then that the annual decline in temperatures begins. It is interesting to observe the close correspondence between this environmental change and the beginning of regrowth of the gonads.

It would seem probable that a marine animal living high in the intertidal zone, as Acmaea persona does, might spawn during a period characterized by unusually high tides since it would only be under such conditions that the animals would be submerged for any length of time. However, the periods of 1950, 1951, and 1952 for which complete spawnings are recorded do not include any extreme tidal fluctuations. Rather, it is the lack of such extremes which is surprising, the highest tide recorded in the three periods being 5.8 feet in 1951. Nor can the stimulus to spawning be attributed to a particular lunar phase since a new moon was in evidence during the 1950 spawning and full moons during both the 1951 and 1952 periods. An analysis of the two periods in 1951 and 1952 when partial spawnings took place shows that tidal fluctuations here contrast strongly with those associated with the periods of complete spawnings just discussed. In 1951 the period of partial spawning included a tidal range of 8.8 feet, which is about a maximum for the San Francisco coastal area. This range occurred at the beginning of the period on January 7 and was associated with a new moon. Toward the end of the 15-day period, the full moon with its

lower tidal range became prominent. Essentially similar conditions prevailed in 1952 during the period of partial spawning except that here the full moon came at the beginning of the period and the new moon at the end.

The mean temperatures for complete spawning periods of the three years are very similar. That of the water shows a variation of only 1.5° F. (52.0° — 53.5°) throughout the three periods while that of the air varied only 1°F. (50° — 51°). It is perhaps the attainment of such specific environmental temperatures which acts as the stimulus for spawning. During the periods of partial spawning the air and water temperatures were below those of the periods of complete spawning. As has been discussed, the partial spawnings appeared to occur within two to four weeks following the development of fully ripe gonads. It is interesting to note that the time required for this development varies from year to year and thus influences the time of the partial spawning. In 1950 fully ripe animals were not found until mid-February and the spawning which followed was a complete spawning, no partial spawning occurring in this year. By contrast, fully ripe animals were present in December 1950, and a partial spawning took place in late January 1951. An intermediate condition was found in 1952 when fully ripe animals were found in late January and a partial spawning took place in late February.

Table 2 summarizes the temperature conditions for October through February of the years 1949-1950, 1950-1951, and 1951-1952. The winter of 1949-1950 was the coldest of the three winter periods, and it was in this season that gonad redevelopment was slowest and a partial spawning was lacking. The comparable period of 1950-1951 was considerably warmer, and a rapid development of the gonads was observed, together with an early partial spawning. The winter of 1951-1952 was again intermediate, both in conditions of temperature and in gonad redevelopment.

On the basis of the seasons of activity of 1950-1951 and 1951-1952, it is evident that Acmaea persona is reproductively active during the period of October to April. The mean surface water temperatures characterizing these months are listed below, together with the corresponding air temperatures. From these data, then, it is assumed that the single complete spawning of the year occurs at a relatively fixed period and is correlated with the appearance of a particular range of environmental temperatures. It is further suggested that go-

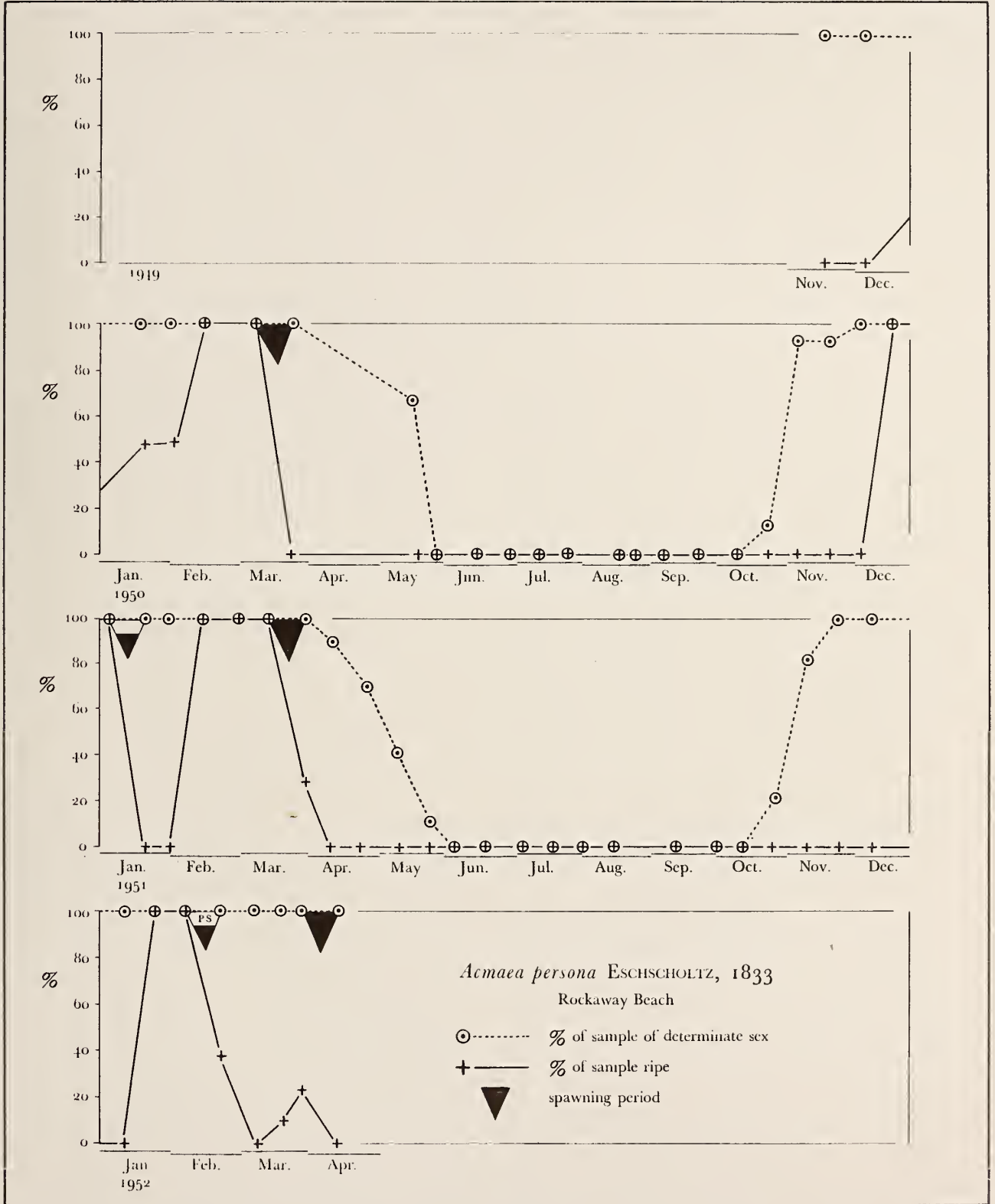


Table 2

Summary of Mean Air and Water Temperatures October through February, 1949 - 1952

	Mean Air Temperature Half Moon Bay			Mean Water Temperature Fort Point		
	1949 - 50	1950 - 51	1951 - 52	1949 - 50	1950 - 51	1951 - 52
October	52.9	57.1	56.1	56.9	58.3	59.1
November	57.9 *	59.3	53.8	54.9	57.5	55.2
December	47.3 *	54.0	49.3	51.5	54.9	52.7
January	44.7 *	49.4	47.3	48.3	50.4	50.4
February	49.7	50.5	50.3	50.0	50.6	52.9
Mean	50.5	54.1	51.6	52.3	54.3	54.1

* Temperatures from Santa Cruz, California (data from Half Moon Bay not available)

nad redevelopment begins shortly after the year's temperature maxima have been passed and that the rate of development thereafter is influenced directly by the temperatures of the winter season. This rate of development determines, in turn, whether or not a partial spawning takes place and the time when it will occur.

	October	April
WATER		
1950-1951	58.3°	52.4°
1951-1952	59.1°	53.8°
AIR		
1950-1951	57.1°	50.7°
1951-1952	56.1°	51.4°

Acmaea fenestrata cribraria CARPENTER, 1857

Ecology: — This species was studied exclusively from the southern point of Rockaway Beach. Here the species is less common than either *Acmaea pelta* Eschscholtz, 1833 or *A. scutum* Eschscholtz, 1833 and occupies an ecologic niche essentially exclusive to itself. It seems to require a substrate of very smooth boulders which do not have macroscopic algae on them. These boulders are typically set in loose gravel and sand, and the animals retreat down the sides of the rocks and are found at low tide grouped in the shaded areas of the boulders with their shells pressed slightly into the gravel. The essential feature of the habitat of this animal at Rockaway Beach is the polished bare rock surface chosen as a substrate. Only rarely is either of the other limpets found in zone 2 or 3 [*A. pelta* or *A. scutum*] observed on these rocks since these two species apparently require the presence of at least some macroscopic algae. From this description it is evident that *A. f. cribraria* is a film feeder and not a browser.

Collections: — This species was studied from a level of about zone 2 where the prevailing algae were *Ulva* and *Petrocelis* or some related encrusting red alga. At this level both *Acmaea scutum* and *A. pelta* were to be found, the former being the more common. The gonad of *A. fenestrata cribraria* does not seem to undergo the extensive growth that is characteristic of *A. persona*. Indeed, the degree of turgor encountered in the *A. fenestrata* gonad is only comparable to that of a partially ripe *A. persona*. Collections were begun on May 5, 1950, and were continued through April 16, 1952, at two-week intervals. Samples consisted of about five animals and a total of 246 limpets was examined: 120 males, 93 females, and 33 indeterminate.

Results: — At the time (Plate 16) that the study was begun, the animals were all in a partially spawned condition. The gonads continued to regress until by June 18, 80 percent of the sample had become indeterminate. Although the two July collections show high percentages of determinate animals, these specimens were all in a spawned condition and did not represent a redevelopment of the gonad. It was not until the collection of August 27 that partially ripe animals were found, and these possessed gonads in the first stages of redevelopment. From this date until November 24, the gonads continued to increase in degree of ripeness until spawning occurred during the last week of November or the first week of December and was continued, probably, to about December 22. Following spawning, a redevelopment was observed until a second spawning occurred during the middle of January. A third and last spawning took place sometime during the last of March, after which the gonads showed a continued regression to the indeterminate condition characteristic of the summer months. There is some

reason to believe that a small spawning took place between the collections made on February 2 and February 18 since the animals found on the earlier date showed at least partially developed gonads while those on the 18th were definitely spawned. The collection of August 18 marked the beginning of gonad regrowth, and this continued at a slow rate through December and early January, the first spawning of 1952 occurring sometime during the last half of January. Between March 10 and 22 a second spawning took place.

Analysis of Environmental Conditions Coincident with Spawning: —

At Rockaway Beach this limpet is reproductively active beginning in late August or early September and continuing until mid-May of the following year. From mid-May until mid-August the animals are reproductively inactive, a large percentage being indeterminate. Approximately a month before the year's temperature maxima are reached the gonads begin to redevelop so that in September all of the animals are of determinate sex and partially ripe. The summer indeterminate period may result from the unfavorable environmental conditions present at that time. The period from May through August is quite warm and is certainly the driest of the year but does not include the warmest month, September. Nor is the beginning nor the end of this phase marked by any striking environmental change. However this may be, the reproductive cycle of *Acmaea fenestrata*, like that of *A. persona*, is marked by an inactive phase during the months when heating and desiccation are near their maxima. *Acmaea fenestrata* can be considered to be reproductively active from August through April or from sea temperature means of the following:

	August	April
1950-1951	60.5°	52.4°
1951-1952	58.0°	53.8°

As has been discussed in relation to *Acmaea persona*, the winter of 1950-1951 was characterized by temperatures somewhat above those of 1951-1952 and the possible relation of this to the rate of gonad redevelopment has been indicated. A similar relationship is seen for *A. fenestrata* since its first spawning occurred in November-December 1950 while the corresponding spawning of 1951-1952 was delayed until January 1952. The effects of tidal activity and lunar phase are impossible to evaluate because of the fact that, except for the spawning of March 18-April 1, 1951, either a new moon

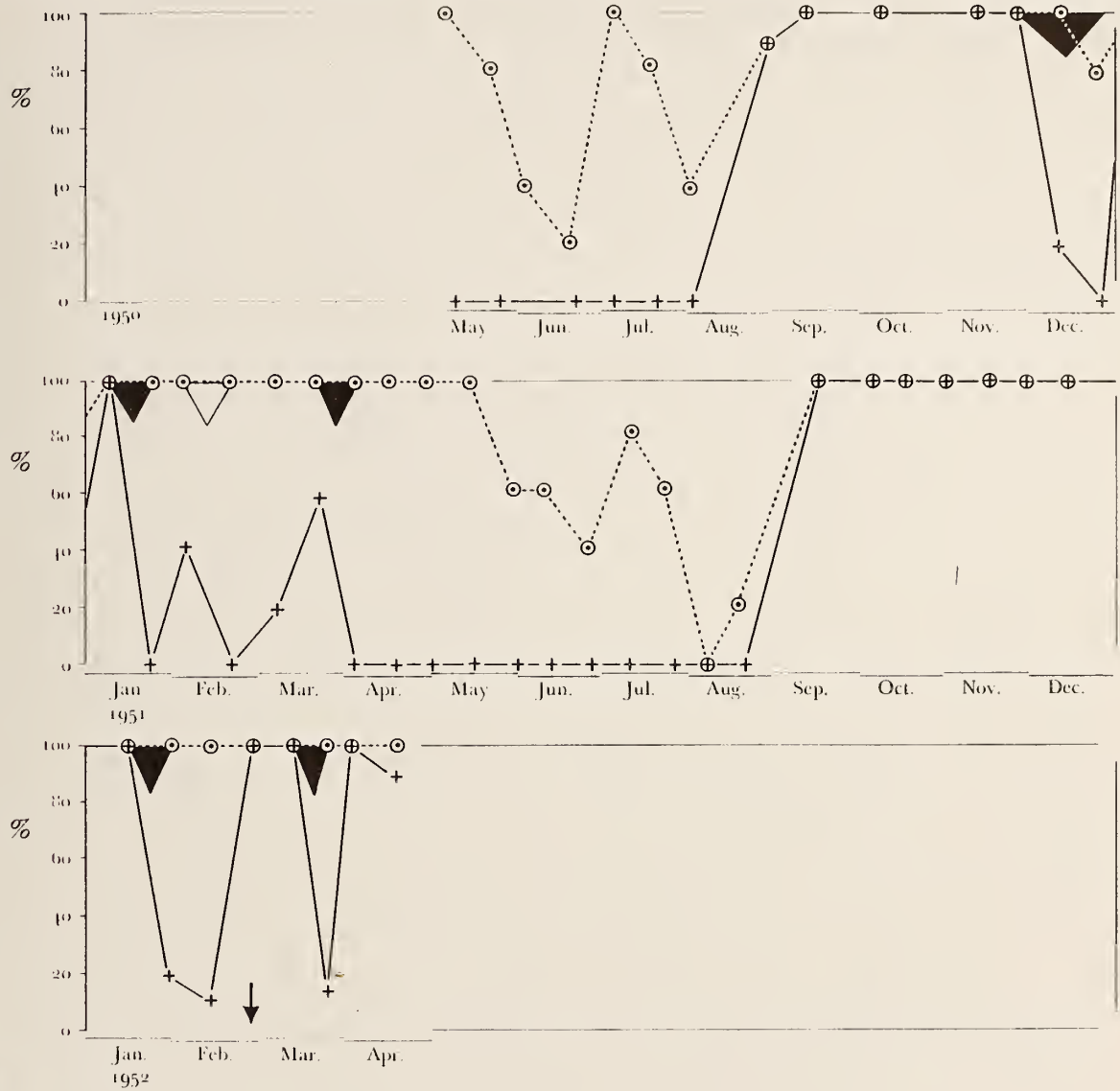
or a full moon was present at the beginning and at the end of the two-week interval between collections. For this reason, it is not known which moon, if either, constituted a stimulus for spawning. This problem will be encountered frequently and is, of course, a result of the necessity of making collections when the tides were favorable for field work. Air and water temperatures seem to bear no relationship to initiation of spawning in this limpet since spawnings are recorded at water temperatures ranging from 50.0°F. to 56.0°F. or over about $\frac{2}{3}$ of the total mean yearly range (51—60°F.). From this study, then, while it has been possible to elucidate the nature of the annual cycle of this limpet at this latitude and to suggest some of the factors which may control it, it has not been possible to analyze successfully the factors which serve as stimuli to spawning.

Acmaea scutum ESCHSCHOLTZ, 1833

Ecology: — This fairly eurytopic species was also studied from the south point of Rockaway Beach where the animals are found in large numbers. As has been stated before, this shore is composed of large boulders set in sand and gravel. At the level of zone 2, where *Acmaea scutum* is most abundant, these boulders have only sparse growths of algae: *Endocladia*, *Ulva*, and in more shaded regions, some *Petrocelis*. In addition to this macroscopic growth, the rocks typically have a greenish sheen caused by a thin film of algae which is also present on the shells of the limpets in somewhat thicker mass. The impression has been gained from this study that *A. scutum* is primarily a scraper of this algal film in contrast to *A. pelta* which seems to require macroscopic algae for food. For this reason, there is a reduced competition between the two species which, at first glance, seem to occupy the same ecologic niche. This does not imply that *A. scutum* will not browse on larger algae if such are present, for it certainly does so in the lower intertidal zones.

Collections: — The first collection of this species was made on September 25, 1949, and collections were continued until April 16, 1952. In all, 1535 animals were examined: 804 males, 684 females, 22 indeterminate, and 25 immature. The sample size was consistently about 25 animals.

Results: — The reproductive cycle (Plate 17) of this species is characterized by several spawnings throughout the year, most of these being partial spawnings. The animals are reproduc-



Acmaea fenestrata cribraria

CARPENTER, 1857

Rockaway Beach

- ⊙----- % of sample of determinate sex
- +——— % of sample ripe or partially ripe
- ▼ spawning period
- ↓ laboratory spawning